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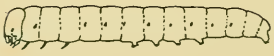

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Linda Butler and Gregory Chrislip

INTRODUCTION

Observations of environmental effects of anthropogenic (human generated) pollution have been made for many years. Several excellent reviews of the effects of pollutants on insects have appeared (Alstad et al. 1982; Heliövarra and Väisänen 1993; Brown 1993; Riemer and Whittaker 1989). Air pollution has been associated with both direct and indirect effects on insects (Alstad et al. 1982).

Direct effects of pollutants may benefit populations of insects [e.g. increased egg survival in pine sawfly resulting from contact of eggs with acid precipitation (Heliövarra et al. 1992)] or produce detrimental effects [e.g. reduced pupal size of noctuid (owlet) moths reared on foliage near industrial sites releasing high concentrations of heavy metals (Heliövarra et al. 1989)].

Indirect effects may result from pollution-induced changes in the balance between herbivores and their predators and parasitoids or changes in the suitability of the host plants (Riemer and Whittaker 1989). While effects close to pollution point sources have been known for many years, more recent reports have indicated more widespread changes in insect herbivory resulting from pollutants (Riemer and Whittaker 1989).

Indirect effects of pollution on herbivorous insects as mediated through their natural enemies is not always predictable. Simulated acid rain increased survivorship of early instar pine sawflies presumably by reducing their susceptibility to viruses (Saikkonen and Neuvonen 1993). On the other hand, leaf beetles

reared on acid-treated birches were more susceptible to ant, carabid and bird predators presumably as a result of decreased defensive secretions (Palokangas et al. 1995).

It is well known that stress, including that produced by ambient chemical substances, alters the biochemical makeup of plant foliage. Stress from a variety of causes results in an increase of soluble amino acids such as arginine and glutamine (Van Dijk and Roelofs 1988; Zedler et al. 1986). Trees stressed by pollutants [or indeed other factors such as drought (White 1974)] show increased levels of nitrogen and increased abundance of herbivorous insects (Heliövarra and Väisänen 1990; Koricheva and Haukioja 1992).

Acidic precipitation is perceived as a significant air pollution problem derived chiefly from fossil fuels, automotive emissions, smelting of sulfide metals and other industrial processes. The northeastern portion of the United States is at the center of the high acid rainfall area in North America (Evans 1984). Recent reports on forest impact of acid precipitation have not been in agreement. Hertel et al. (1993) concluded that there is no evidence of general, widespread decline of forests due to acid deposition. However, surveys of 200 hardwood forest plots across a west to east acid precipitation gradient in Pennsylvania showed that, for trees, growth rates decreased and mortality rates increased between the early surveys of the 1960s and 1970s and a 1985 survey (Brooks 1994).

One method to evaluate acidic deposition effects on forest ecosystems is whole-watershed manipulation, i.e. applying a potentially acidifying agent to one watershed and comparing the results with an untreated reference watershed (Adams et al. 1995). In 1989, a watershed on the Fernow Experimental Forest near Parsons, WV, was designated for experimental acidification and initial treatments were begun. During the growing seasons of 1993 and 1994, we sampled canopy arthropods in the treated watershed and a nearby reference watershed and compared their

richness (number of arthropod families or species) and abundance. We evaluated distribution of the arthropods by feeding guild and analyzed amino acid levels in foliage. This was an unreplicated study, and therefore no statistical analysis was conducted. Because of their expense, whole-watershed experiments are not often replicated (Adams et al. 1995).

MATERIALS AND METHODS

The study was conducted on the Fernow Experimental Forest in north-central West Virginia. This forest is located on the unglaciated Allegheny Plateau (latitude 39° 95' N, longitude 79° 41'W) at elevations ranging from 533 to 1,112 m. The topography is rugged with slopes of 10 to 60 percent. The experimental forest encompasses 1,902 ha and has been divided into a series of watersheds for research purposes (Northeastern Forest Experiment Station 1987). This study was conducted on watersheds 3 and 5 (map in Adams et al. 1993).

Prior to establishment of the Fernow Experimental Forest in 1934, the site was heavily logged between 1905 and 1910. Additional thinnings for research occurred on several of the watersheds from the early 1950s through the late 1970s. Common tree species now on the better quality sites include yellow-poplar (*Liriodendron tulipifera* L.), sugar maple (*Acer saccharum* Marsh), black cherry (*Prunus serotina* Ehrh.), white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.) and Northern red oak (*Quercus rubra* L.). Dominant tree species on the poorer quality sites include various species of oak (*Quercus* spp.), hickory (*Carya* spp.), sourwood [*Oxydendrum arboreum* (L.) DC] and sassafras [*Sassafras albidum* (Nutt.) Nees] (Adams et al. 1994).

Watersheds 3 and 5 have many similar features. Both are underlain by Hampshire Group bedrock geology. The Hampshire Group includes the Rowlesburg and Canon Hill

Formations. The dominant soil on WS3 and WS4 (that lies adjacent to WS5) is a Calvin channery silt loam (loamy-skeletal, mixed, mesic Typic Dystrochrepts). Since other watersheds that lie on Fork Mountain (the location of WS3 and 5) have the same soil series, WS5 is believed to have a Calvin channery silt loam as its dominant soil type also (P. Edwards, personal communications; Adams et al. 1995).

The topography on both WS3 and WS5 is similar; ridgetops and valleys are narrow and side slopes are relatively steep. Average slopes on both watersheds are 20%. Elevation on WS3 ranges from 735 to 860 m and on WS5 from 724 to 829 m.

Watershed 3 received selective cuts in the 1950s and 1960s and was clearcut to 2.54 cm diameter in 1970. Watershed 5 has two distinct areas that have been subjected to uneven-aged management. WS5A (31.7 ha) was cut in 1958, 1968, 1978 and 1987. WS5B (5.8 ha) was cut in 1958, 1968 and 1983. Cuts on both areas were selective cuts in which trees over 27.9 cm dbh were removed (Adams 1995; P. Edwards, personal communication.) Other comparisons for WS3 and WS5 are given in Table 1.

Watershed 3, the experimentally acidified watershed, received March and November applications consisting of 33.6 kg of ammonium sulfate fertilizer per hectare beginning in 1989, an amount corresponding to 8.1 and 7.1 kg ha^{-1} of S and N, respectively. Each July, 100.8 kg of fertilizer per hectare or 24.4 and 21.2 kg ha^{-1} S and N, respectively, was applied. All applications were made by helicopter. The above application rates were approximately double the amount of S and N deposited on the watersheds in throughfall, believed to be a good estimate of bulk deposition. Therefore, the total amounts of nutrients deposited annually on the treated watershed were 60.5 kg S (ambient S + 40.6 kg from treatment) and 53.8 kg N (ambient N + 35.4 kg from treatment) per hectare or approximately three times that received by the reference

Watershed 5 (Adams et al. 1995).

To compare the two watersheds, arthropod richness and abundance on foliage of red maple and black cherry were assessed. Sampling consisted of pole pruning of 4 samples each of red maple and black cherry within each watershed each week (16 samples per week) from 12 May to 15 September 1993 and from 12 May to 29 September 1994 giving a total of 640 samples for the study.

In the laboratory, all arthropods were removed from the foliage and identified to family with the exception of the macrolepidoptera larvae that were identified to species. All leaves were removed from twigs, oven dried and weighed; foliage samples were standardized as 50 g of leaf weight. Comparisons were made between watersheds 3 and 5 of arthropod family richness and abundance and species richness and abundance of macrolepidoptera.

A computer file was created dividing all families of canopy arthropods taken in this study among canopy arthropod feeding guilds using an arrangement modified from Moran and Southwood (1982). Feeding guilds are groups of families or species that exploit the same food resources in a similar manner (Root 1967). A comparison was made of the abundance of arthropods per feeding guild per watershed.

On June 1 and August 10, 1994, foliage samples from 20 trees each of black cherry and maple were collected from WS3 and WS5 and immediately put on ice in a cooler. In the laboratory, leaves were removed, cut into 2 cm pieces and freeze dried. Samples were sent to the Biotechnology Analytical and Synthesis Facility at Cornell University for amino acid analysis. At the laboratory, the samples were ground to a fine powder and amounts ranging from 36.2 mg to 46 mg were weighed into 15 ml centrifuge tubes; 10 ml 20% CH3OH/0.1 N HCL was added to the tubes and extracted via sonication and vortexing over a

period of several hours. Extracts were kept at 4°C overnight; a small aliquot was removed and centrifuged at high RPM to separate fines. The resulting supernate was the working sample from which aliquots for analysis were removed. One sample was prepared in duplicate to determine reproducibility while two of the original extracts were further treated on a C-18 Sep-Pak (a disposable HPLC cartridge) to enhance the eventual analysis (Robert Sherwood, Cornell University, personal communication).

RESULTS

Results of the study on canopy arthropod richness and abundance in WS3 and WS5 are given in Table 2. No difference in arthropod richness is noted between the two watersheds. For both years of the study, however, arthropod abundance was higher on WS3 (27% higher in 1993 and 21% in 1994). As we reviewed the various arthropod families, most groups seemed to show little difference in abundance between the watersheds. Differences appeared to be present in certain families of leaf chewers and juice feeders. While the abundant juice-feeding family Miridae showed no difference (or greater abundance on WS5 in 1993), the related family Tingidae was consistently more abundant on WS3. Among the juice-feeding Homoptera, no difference in abundance was seen for Cicadellidae but Aphididae were 54% more numerous on WS3 in 1993 and the related Psyllidae were much more abundant on WS3 for both years. Among the leaf-chewing Coleoptera, the major families Curculionidae and Chrysomelidae were considerably more abundant on WS3: 86% greater for Curculionidae and 83% greater for Chrysomelidae, for both years combined. Both macrolepidoptera and microlepidoptera were consistently more abundant on foliage of WS3: 34% greater in 1993 and 16% greater in 1994.

In assessing distribution of canopy arthropods among feeding guilds, it is apparent that differences in abundance between

watersheds occurred almost exclusively within the phytophages, particularly the chewers (Table 3). For both years combined, the chewing phytophages were 69% more abundant on WS3 while on the same watershed the sapsucking phytophages were 18% more abundant. No corresponding difference between watersheds was seen among the predatory insects, but parasitic wasps were noted to be 36% more abundant on WS3. Epiphytic arthropods, those that feed on lichens and fungi, were 21% lower in abundance on the acidified watershed.

Results of analysis of free amino acids in foliage of black cherry and maple from WS3 and WS5 for June and August sample periods are given in Tables 4 and 5. Aspartic acid, glutamic acid, glutamine, arginine and proline were higher in black cherry foliage on WS3 (Table 4) during June and August. The differences were particularly great for aspartic acid in August, glutamic acid in August and arginine in June. Alanine was higher on WS3 in August but not in June. For red maple (Table 5) such differences in quantities of amino acids were not observed. Aspartic acid was slightly higher in maple foliage on WS3 in August.

Examination of distribution of arthropod richness and abundance by tree species in this study showed little difference in richness but a somewhat greater abundance of arthropods on foliage of black cherry than maple, particularly for 1993 (Table 6). Abundance of arthropods per watershed per tree species, for both years combined, indicated the highest abundance overall is on cherry on WS3 (Table 7).

DISCUSSION

The term "air pollution" covers a wide range of anthropogenic, atmospheric contaminants such as particulate matter, fluorides, ammonia, volatile organic compounds, carbon monoxide, hydrogen chloride, chlorine, radioactive substances, carbon

dioxide, and acid rains (Brown 1993). Atmospheric acidification results from the emission of several reducing molecules (e.g. SO_2, NO_2) during the combustion of fossil fuels and related photochemical processes that reinforce each other in a complex manner. The anthropogenic release of sulfur and nitrogen oxides has increased the acidity of precipitation 10 to 100 times compared to preindustrial levels (Heliövarra and Väisänen 1993). Deposition of acidic materials can be "dry" (particulate) matter or "wet" (molecules washed out through precipitation), and the pattern of deposition varies according to the seasonal direction of the prevailing winds and the source of pollution (Heliövarra and Väisänen 1993).

Oxides of sulfur and nitrogen consistently increase the performance of herbivorous insects, presumably indirectly through an effect on host plants (Brown 1993). Accumulation of certain plant foliar amino acids (arginine, glutamine, and proline) can be used as indicators of anthropogenic and natural stressors including atmospheric deposition of nitrogen (McLaughlin et al. 1994).

Numerous studies of indirect effects of air pollution on insects have appeared in recent years. Simulated acid rain reduced susceptibility of pine sawfly larvae to their specific NPV viruses (Neuvonen et al. 1990). Differences in impact of acid precipitation occur among species of forest trees. Simulated acid rain negatively affected gypsy moth larvae fed white oak foliage but positively affected larvae fed red oak foliage (Cannon 1993). Outbreaks of pine moths are known to increase in areas with intermediate concentrations of air pollutants (Heliövarra and Väisänen 1986). Lepidoptera may do best on inferior foliage either because of a reduction of their natural enemies or through decreased resistance of host trees (Heliövarra et al. 1989). Aphids tend to increase their growth rate on SO_2 and NO_2 fumigated plants (Houlden et al. 1990). Mexican bean beetle growth was found to be stimulated by feeding on SO_2 fumigated plants (Hughes et al. 1985). Borer injury increased at high

deposition and thrips at low deposition portions of a wet sulfate/pH gradient in Pennsylvania (Nash et al. 1992). Houlden et al. (1990) suggested that there may be a common underlying mechanism by which air pollution enhances insect performance, irrespective of feeding strategy. Moderately stressed plants appear to become more susceptible to herbivores because of increased nutritional value and reduced defenses (Koricheva and Haukioja 1992). For example, free amino acid levels that were found to increase in stressed plants enhanced herbivore growth (Rao et al. 1990).

Most studies of insects and air pollution effects have dealt with individual species whether in laboratories or field studies. We attempted to examine impacts on the forest canopy arthropod complex which consists of hundreds of species. In addition, the above cited studies were conducted with SO_2 or NO_2 fumigated plants, SO_2 or NO_2 industrial emission in the field or simulated acid precipitation. In all cases, contact occurred between foliage (and arthropod) and the gaseous or aqueous pollutant in question. In our study at the Fernow Experimental Forest, we attempted to determine the effects of experimental acidification following application of dry ammonium sulfate fertilizer to the soil. While the ammonium sulfate was applied by helicopter, the dry granules did not adhere to the foliage but passed directly to the soil. Therefore any effects observed should be strictly from increased soil acidity and impact through root systems.

Measurements of soil leachate chemistry, including pH, for WS3 have not been published (P.J. Edwards, personal communication). The pH for A-horizon and B-horizon soil water did not change significantly between 1988 and 1993, and considerable seasonal fluctuation occurred during each year. The soil water pH has shown a downward trend, however.

Since our study was unreplicated, only trends can be noted. The trend was for total canopy arthropods to be more abundant on foliage in the acidified watershed, WS3. In 1993, arthropods

were 26% more abundant on black cherry and maple foliage of WS3; in 1994, this difference dropped to 21%. The arthropods contributing most to this greater abundance were the herbivores, especially the chewing insects, Coleoptera and Lepidoptera. The sapsucking aphids were considerably more abundant on WS3 in 1993; Psyllidae were more abundant on WS3 in both years.

Neuvonen and Lindgren (1987) were the first to show an interaction between the effects of acid rain and drought on reproduction in aphids. Aphids produced 40-100% more progeny on birches watered with dilute sulphuric acid than on control trees. The reproduction of aphids on acid-treated birches was enhanced when precipitation was below long-term average, suggesting an interaction between stress caused by acid treatment and dry periods (Neuvonen and Lindgren 1987).

Since we found a notable shift in proportion of aphids on WS3 and WS5 between 1993 and 1994, we obtained precipitation data for the Fernow Experimental Forest (USDA Forest Service 1995). These precipitation measurements were obtained from a weather station on watershed 4 adjacent to the location of our study. Rainfall in 1993 was 16.46 in. February through April, 10.02 in. May through June, and 5.13 August through October. For 1994, rainfall was 21.62, 22.29 and 9.55 during those time periods, or 23% higher than in 1993. Perhaps the relatively high aphid abundance on WS3 in 1993 reflected a synergism between acidification and drought.

Epiphytic arthropods, those feeding on lichens and aerial fungi, were 21% less abundant on WS3. Epiphytic fungi are considered to be sensitive to acid rain (Ranta 1990). The frequencies of pollution-sensitive species of epiphytic lichens have decreased in Finland between 1967 and 1985 (Kuusinen et al. 1990). André (1985) suggested that changes in communities of corticolous (bark inhabiting) microarthropods should parallel that of epiphytic lichens. Perhaps the lower abundance of epiphytic arthropods found on WS3 reflects a reduced quantity or quality

of epiphytic host material.

Of the various explanations for the greater abundance of herbivorous arthropods on foliage in acidified watershed 3, we suggest that higher levels of certain amino acids in black cherry foliage account for the greatest differences in abundance. This foliage had consistently higher levels of soluble amino acids, particularly aspartic acid, glutamic acid, glutamine, arginine and proline. These amino acids provide an important part of the nutrition of these herbivores which may results in increased reproductive capacity and/or survival. Numerous studies have concluded that higher levels of soluble amino acids in foliage promote growth and reproduction in insects (Riemer and Whittaker 1989; Heliövarra and Väisänen 1993).

SUMMARY

Anthropogenic pollution produces a variety of effects, both direct and indirect, on insect populations. In 1993 and 1994 we evaluated richness and abundance of canopy arthropods within and between experimentally acidified (WS3) and reference (WS5) watershed. Experimental acidification was accomplished by the aerial application to WS3 of ammonium sulfate fertilizer equivalent to three times the N and S received by natural throughfall within the control watershed. Fertilization occurred three times each year beginning in 1989 and continuing throughout the study.

We sampled canopy arthropods by pruning of foliage. All arthropods were determined to family except macrolepidoptera larvae that were identified to species. We also analyzed quantity of free amino acids in foliage of black cherry and red maple in June and August 1994. Arthropod abundance was 27% and 21% higher in WS3 and WS5 in 1993 and 1994, respectively. The greatest differences occurred among the herbivorous arthropods, especially the chewers (macrolepidoptera, Curculionidae,

Chrysomelidae). Overall, the highest abundance of arthropods occurred on black cherry on WS3. Amino acid analysis showed black cherry on WS3 to have the highest level of free amino acids, especially aspartic acid, glutamic acid and arginine. The greater nutritional value of cherry foliage may account for the higher arthropod abundance.

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Figure 1. Major experimental watersheds and streams on the Fernow Experimental Forest (Adams et al. 1994).

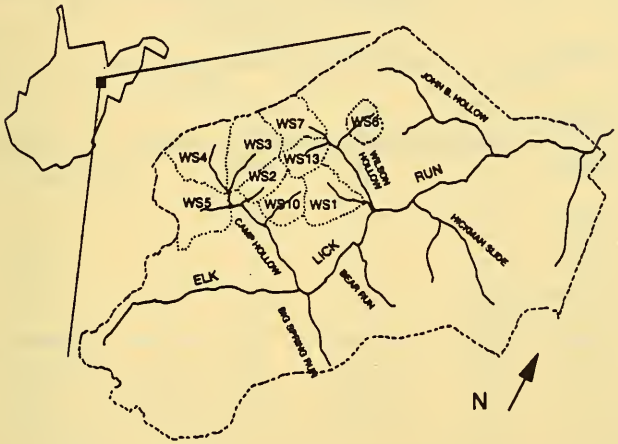

Table 1. Characteristics of two experimental watersheds on the Fernow Experimental Forest, West Virginia.

	Watershed			
Characteristic	3	5	5A	5B
Area (ha)	34.3	36.4		
Aspect	S	NNE		
Site Index	74		75	64
Stand Density (trees ha^{-1})	538		253	371
Dominant Tree Species	black cherry		sugar maple	Northern red oak
	red maple		American beech	chestnut oak
	black birch		Northern red oak	American beech
	American beech		red maple	red maple

Table 2. Richness (R) and abundance (A) of arthropods taken from foliage of red maple and black cherry on the experimentally acidified (WS3) and reference (WS5) watershed at Fernow Experimental Forest in 1993 and 1994. Figures for abundance represent total individuals

	1993		1994	
Taxon	WS3	WS5	WS3	WS5
Arthropod Family R	92	101	96	89
Arthropod A	5,689	4,193	5,894	4,659
Hemiptera A				
Miridae	538	855	523	596
Tingidae	35	5	107	4
Homoptera A				
Cicadellidae	250	241	471	362
Aphididae	239	111	265	362
Psyllidae	597	53	97	14
Coleoptera A				
Curculionidae	944	141	733	99
Chrysomelidae	219	47	297	40
Lepidoptera A				
Macrolepidoptera	721	566	749	698
Microlepidoptera	785	425	357	227
Total Lepidoptera	1,506	991	1,106	925

Table 3. Abundance of arthropods among feeding guilds in black cherry and maple canopies of WS3 and WS5 for 1993 and 1994 combined.

Guild[1]	WS3	WS5
Phytophages (chewers)	3,541	1,105
Phytophages (sapsuckers)	3,195	2,633
Epiphytes	724	917
Scavengers	119	69
Predatory Insects	1,149	1,098
Predatory Arthropods	2,134	2,388
Parasitoids	271	174
Ants	139	235
Tourists	268	206

[1] Modified from Moran and Southwood

Table 4. Quantities of free amino acids in black cherry foliage from acidified watershed 3 and reference watershed 5 in samples taken in June and August, 1994.[1]

	June		August	
Amino Acid	WS3	WS5	WS3	WS5
Aspartic Acid	156	132	210	115
Glutamic Acid	224	111	259	155
Glutamine	42	20	42	17
Arginine	430	39	191	30
Alanine	73	71	162	96
Proline	38	22	61	18

[1] Each figure represents mean of three analyzed aliquots (in pmols)

Table 5. Quantities of free amino acids in red maple foliage from acidified watershed 3 and reference watershed 5 in samples taken in June and August, 1994.[1]

	June		August	
Amino Acid	WS3	WS5	WS3	WS5
Aspartic Acid	72	93	130	99
Glutamic Acid	151	167	97	106
Glutamine	11	16	19	13
Arginine	19	39	23	20
Alanine	33	31	52	76
Proline	8	9	11	9

[1] Each figure represents mean of three analyzed aliquots (in pmols)

Table 6. Richness and abundance of arthropods by tree species on combined watersheds for 1993 and 1994.

	1993		1994		
	Richness	Abundance	Richness	Abundance	Mean Tree Species
Cherry	93	5,093	93	5,393	5,243
Maple	104	4,789	92	5,159	4,974

Table 7. Arthropod abundance per watershed per tree species for 1993 and 1994 combined.

WS	Tree Species	Abundance
3	cherry	3,196
5	cherry	2,047
3	maple	2,595
5	maple	2,379

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